ORIGIN AND DEVELOPMENT OF THE LAMELLAE IN SCHIZOPHYLLUM COMMUNE

By J. F. Adams

Columbia University

(with plate 9)

Fries ('15) in establishing the genus *Schizophyllus* which he later ('21) changed to *Schizophyllum* says that it is to be distinguished from *Agaricus* and *Merulius* by the longitudinal splitting of the gills with the resulting halves becoming revolute.

Hoffman ('60) describes the carpophores as consisting of lamellar systems which correspond to the crenatures of Buller ('09). The smaller secondary gills are often but not always divided. He believes that the upper surface of the carpophores should be regarded as a "pellicula" comparable to the velum.

Winter ('84) and de Bary ('87) add nothing of consequence to the description by Hoffman.

Fayod ('89) includes *Schizophyllum* in the tribe "Panoides" with *Panus* as representative of the gymnocarpus type. He noted that the young lamellae are entire and held that the splitting was hygroscopic.

Buller ('09) is quite explicit as to the origin of the gills. He says in substance:

"The under layer of the pileus is produced downwards to form the gills. Whilst a pileus is extending by marginal growth, the interlamellar spaces gradually widen. When a space has attained a certain width, it becomes divided into two down the middle, owing to the formation within it of a new gill which arises as a short median downgrowth from the pileus flesh. The splitting of the gills permits the hymenial surfaces being protected during periods of drought. The recurving of the gill plates may be partly explained when a fruit body dries up by the cell walls of the hymenial and sub-hymenial layers contracting much more strongly in the vertical direction than those of the tramal layer."

There is no clear account of the early stages of gill formation in the literature and I have undertaken to fill this gap by the present study. The nature of the whole carpophore also becomes much clearer with a knowledge of the method of origin of the gill.

MATERIALS

Carpophores of *Schizophyllum commune* for this study were collected in the field and also grown on agar. Lima-bean agar, prune agar, and dung agar were favorable media. The cultures were grown in flasks of 50 c.c. and 250 c.c. capacity. Cultures were started from immature carpophores collected in the field, which were washed in distilled water before being transferred to the flask.

Within five days after the carpophores are planted on it the agar surface is covered with a dense white growth of mycelia. The hyphae in cultures are conspicuously branched and microscopical examination shows numerous clamp connections. The hyphae average 3 μ in diameter.

Dense aggregations of buttons often develop over the agar surface. From the cut end of the carpophores and from their margins small buttons are first formed. A number of the buttons when they are in dense clusters fail to mature. Numerous abnormal forms appear, as has been reported also by Miss Wakefield ('09). In some cases an immature carpophore that is transferred to agar will continue its normal development by marginal growth and form a large normal fruit-body (PL. 1, FIG. 1).

Various stages in the development of the carpophore were fixed for study in Flemming's medium mixture, dehydrated, and embedded in 52 paraffin. Sections were cut from 6 μ to 12 μ in thickness.

THE YOUNG CARPOPHORE

The young button appears as a dense, globular mass of intertwined hyphae raised above the substratum. As noted, they often appear in clusters. These carpophore primordia later become differentiated into cylindrical outgrowths which enlarge radially at their outer end. They vary in length from about 1 to 10 mm. and up to 5 mm. in width at the tip.

They are clothed with a loose outgrowth of hyphae from their earliest appearance. These hyphae are thick-walled and no branching was observed. Clamp connections or cross-walls were not found in these superficial hyphae.

Transverse vertical sections of young buttons show a dense homogeneous mass of intertwined hyphae developing parallel with the elongating axis of the primordium. The hyphae show conspicuous clamp connections. The carpophore primordia are of leathery consistency and show no evident differentiation until the appearance of the hymenium primordium.

THE HYMENIUM

In young buttons the first appearance of the fruiting layer is just below the upper end. It consists of a growth of densely staining hyphae. Horizontal sections show this first structure or plectenchyma of hyphae centrally located. With further growth of the carpophore primordia they become somewhat elliptical in outline. The individual hyphae now become oriented, their free ends converging towards the center of the mass.

The first gill cavity is formed in this hymenium primordium. The oldest primordia are in the central part and the youngest towards the sides, showing the order of their formation (TEXT-FIG. A, NO. 2).

The whole carpophore enlarges and as result of growth tensions the gill cavities appear in the center of these primordia of the hymenium. The gill cavities are lined from the first by a palisade layer. The palisade layer is increased by the intercalary addition of new elements with the further increase in size of the gill cavity. The elongated cells composing the palisade layer stain deeply and appear to arise as a system of short branches from the subjacent hyphae which are to form the trama.

The gill cavities thus represent from the first the space between the adjacent halves of two lamellae. The hymenia are oldest toward the base and less undifferentiated toward the tip of the carpophore.

In two instances gill cavities were observed developing in the trama of the matured lamellae. It was observed several times that the inner surface of the gill cavity before maturity was not completely covered by the palisade layer. This condition is found usually along the lower edge of the gill cavity, but the condition becomes normal with the maturity of the gill cavity (PL. 1, FIG. 4). The wall between two adjacent gill cavities is occasionally quite weakly developed owing to the close proximity in their origin.

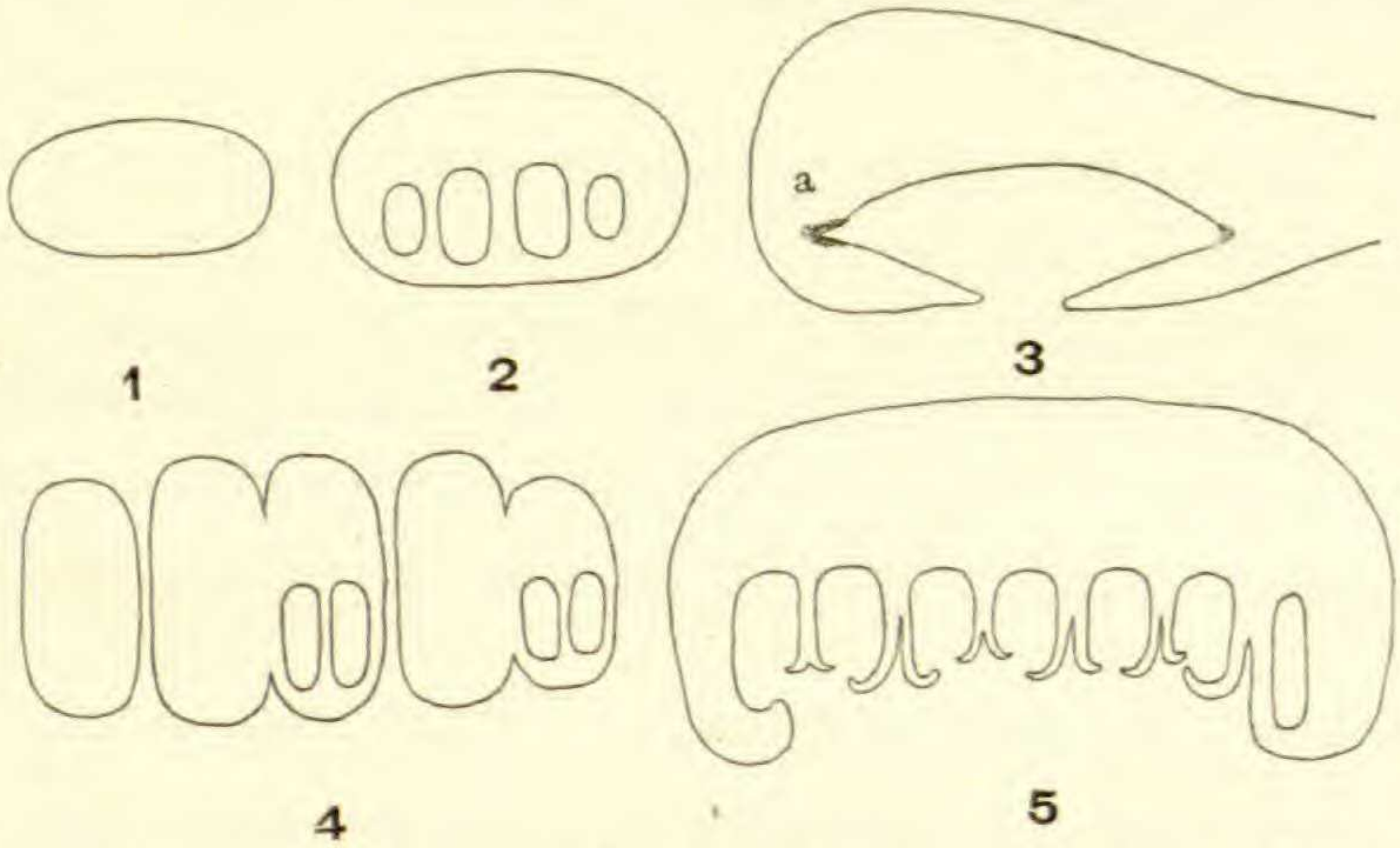

FIG. A. Diagrams of sections illustrating different stages of development of the early carpophore. 1. Transverse vertical section of a button in which no differentiation has appeared. 2. Section cut as above showing later stage with four endogenous and separate gill cavities, the lateral ones younger. 3. A longitudinal median section through a young carpophore showing one of several gill cavities which have opened longitudinally below. *a*, Region of extension of the hymenium primordium. 4. Transverse vertical sections through the apical growing region of the carpophore, showing the origin of the crenatures, two of which are already separated by clefts extending to the dorsal surface of the carpophore. The middle and outer crenatures at right show gill cavities comparable to those in Fig. 4, Pl. 1. In the case of the others, similar gill cavities appear in sections nearer the base of the pileus. 5. Transverse vertical section like those of Buller through the median portions of a carpophore, showing a series of young lamellae, the gill cavities open below except in the case of the one at the right. The gills already show more or less of the characteristic splitting.

In such instances the separating wall, which would normally become a lamella, gradually thins out and disappears. Instead of two gill cavities normally maturing they become one by the abortion of the separating wall.

THE LAMELLAE

The gill cavities split along their lower edge and lamellae are thus completed. They consist, as noted, of the adjacent walls of two gill cavities which originate endogenously as tubes in the substance of the carpophore.

The tissue above the gill cavities already formed increases by intercalary growth and in general the gill cavities lie much nearer the ventral than the dorsal surface of the carpophore. The tissue below the gill cavity appears gradually to become looser in texture as the gill cavity gets larger and this favors the splitting by which the edges of the gills are set free.

Owing to the method of their origin the margins of the lamellae are never entire, but appear irregular and frayed out. The final splitting of the lamella is apparently a hygroscopic phenomenon as described by Buller ('09). The trama is continuous with the tissue of the pileus above the gill. In transverse sections of the lamellae the split is seen to be parallel with the elongated hyphae of the trama, as seen in PLATE I, FIGURE 7.

FURTHER DEVELOPMENT OF THE CARPOPHORE

The growth of the carpophore is marginal and the lamellae are extended in length by the elongation of the gill cavities and the palisade layer in the interior *pari passu* with the development of the carpophore.

In the young immature carpophores after several lamellae have been formed the margin becomes divided into the crenatures. These crenatures are due to the development of a cleavage lamella splitting in certain cases clear through the dorsal surface of a pileus (TEXT-FIG. A, NO. 4). They not only include the primary gills but allow for the origin of new gills on either side in the usual way. The later-formed lamellae are narrower and thus we get the lamellar systems of Fries and the fasciculi of gills of Buller. The pileus enlarges by the continued growth of the primary lamellae and the successive development of additional lamellae, all of which have their origin from gill cavities in the manner described. The more central crenatures are the oldest and the younger are towards the sides of the pileus.

In mature carpophores it is often observed that a short gill appears isolated between the right and left halves of the adjacent lamellae (TEXT-FIG. B, *c*). At the point where such a lamella originated the crenature was increasing in width. The new lamella was continued from its point of origin so long as the growth of the crenature allowed for its development. After attaining a certain width the crenatures gradually become narrower and thin out at the margin. Under such conditions of limited growth some of the enclosed lamellae in the crenature can no longer be continued and do not reach the margin of the crenature. In the mature carpophore the margin is always thinned out and the gills thus become lanceolate in form.

DISCUSSION

In recent years considerable advances have been made in our knowledge as to the origin and development of the lamellae in

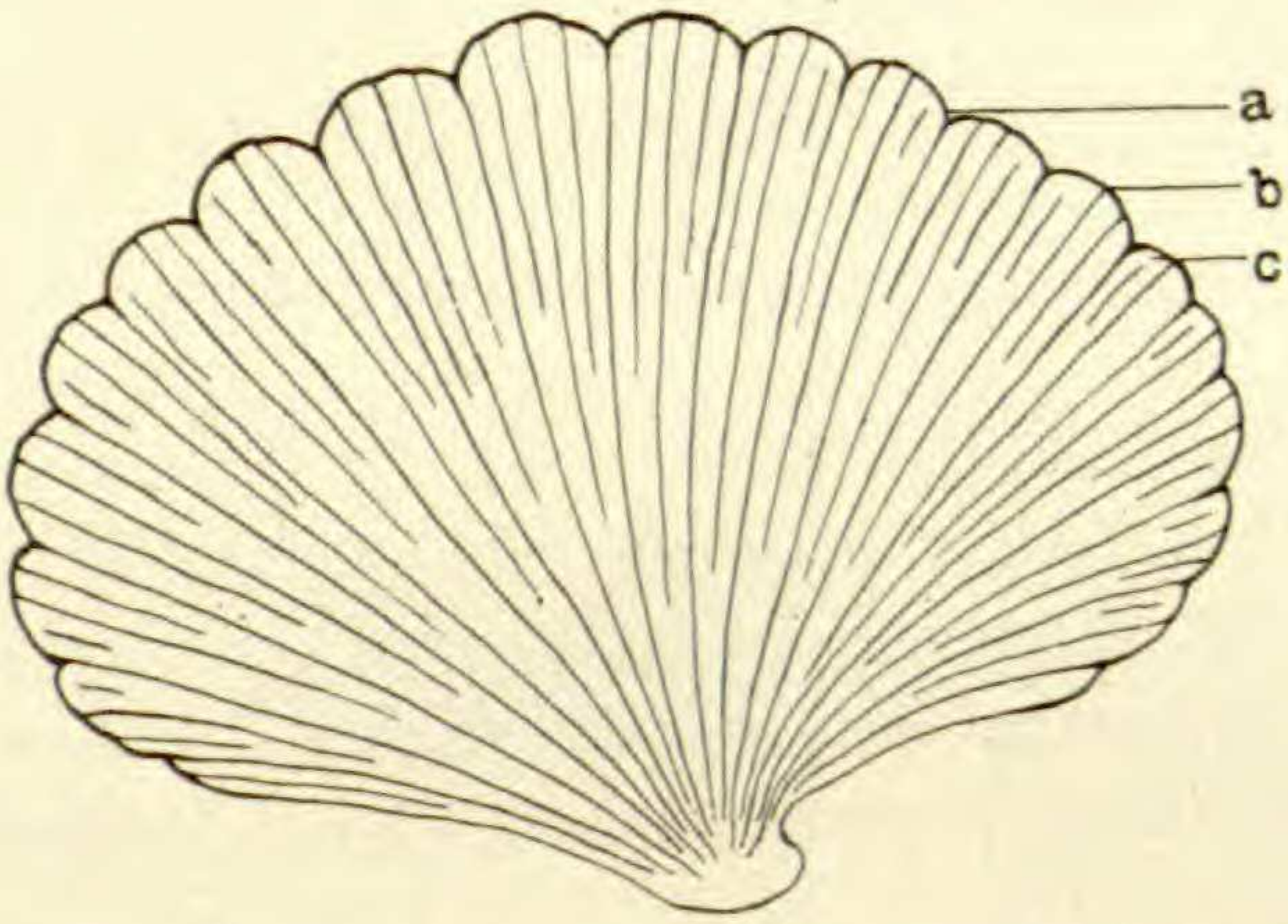

FIG B. Diagram of ventral surface of carpophore showing arrangement of crenatures and gills. *a*, primary gill; *b*, secondary gill; *c*, a disconnected secondary gill.

different members of the Agaricaceae. The endogenous origin of the lamellae has been firmly established for a number of forms.

In *Schizophyllum* the lamellae originate by the formation of endogeneous gill cavities in a fashion similar in principle to that which Levine ('14) finds in *Coprinus micaceus*. They are developed simultaneously in *C. micaceus*, while in *Schizophyllum* they are successively formed. In both cases a series of gill cavities are produced which represent the space between the adjacent sides of a pair of lamellae. There is no general gill cavity into which the lamellae grow downward. In *Schizophyllum*, owing to its habit of growth, this method of origin of the gill cavities as independent tubes is diagrammatic in its simplicity and whether *Schizophyllum* is a progressive or a reduced type we have in it the evidence that gills in their essential nature are hymenium-bearing plates between independently originating endogenous gill cavities.

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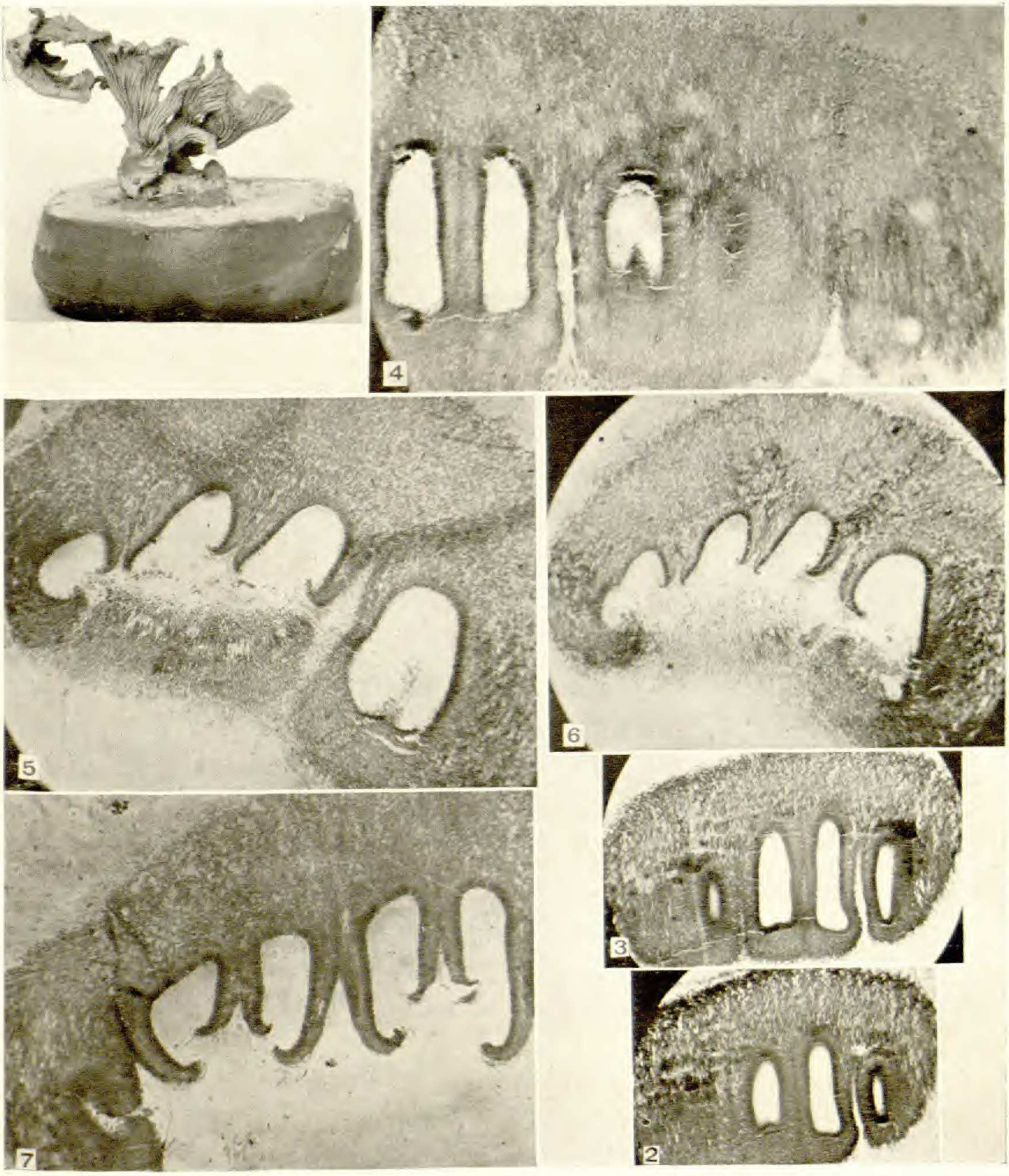
EXPLANATION OF PLATE 9

FIG. 1. A carpophore thirty-four days old, grown from a piece of *Schizophyllum commune* transferred from a branch of birch. 6/13 of the natural size.

FIGS. 2 and 3. Transverse vertical sections through three crenatures of a carpophore with gill cavities in different stages of development. Fig. 3 is further back from growing region than Fig. 2. The gill cavities are seen to lie nearer the ventral than dorsal surface. Photomicrograph × 26.

FIG. 4. Transverse vertical section through the growing region of a carpophore, showing only three crenatures as indicated by the two ventral furrows. The first crenature to the right shows undifferentiated tissues. In the middle crenature appears an imperfectly developed gill cavity and a closed hymenium primordium in which a gill cavity will appear. The crenature on the left shows two mature gill cavities. Photomicrograph × 43.

FIGS. 5 and 6. Sections cut as above, slightly oblique through young carpophore in which gill cavities are open, showing three gills that have split along their lower



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